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THE FORMATION OF SEPTA IN THE FIBER-TRACHEIDS OF *Hypericum Androsaemum* L.

BY

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ALTHOUGH the presence of nuclei in fibers has been established (9, p. 56), the work of Bailey (6), Goldstein (12), Wareham (16), and Esau (10) suggests that the apparent occurrence of the multinucleate condition in fibers is due to a misinterpretation of the material, except in the phloem. As far as we are aware, no description has been given of a division of the protoplast in a fully developed cell to form a nucleated septate fiber-tracheid.

The definition of a septate fiber-tracheid, now widely accepted, is "A fiber-tracheid with thin, transverse walls across the lumen. (In these elements the protoplast divides after the formation of the secondary wall. The septa are true walls)" (8). This definition recognizes the septate fiber-tracheid as a distinct modification of the fiber-tracheid, which in turn is transitional between a tracheid and a libriform fiber. The presence of nuclei during the early stages of maturation is assumed but not stated.

In an earlier paper (15) it was reported that the fiber-tracheids present in the secondary wood of the genus *Hypericum* are septate or non-septate and typically contain a nucleus. Occasionally the nucleus was seen in

EXPLANATION OF THE ILLUSTRATION

FIGURE 1. Typical nucleus in fiber-tracheid. $\times$ ca. 2160.

FIGURE 2. Metaphase division figure in fiber-tracheid.
 $\times$ ca. 2160.

FIGURE 3. Anaphase division figure in fiber-tracheid.
 $\times$ ca. 2160.

FIGURE 4. Telophase division figure in fiber-tracheid.
 $\times$ ca. 2160.

FIGURE 5. Rate telophase division figure in fiber-tracheid. $\times$ ca. 2160.

FIGURE 6. Portion of septate fiber-tracheid, showing septum and two nuclei. $\times$ ca. 1410.

These drawings were made with an Abbé camera lucida at table level.



1



2



3



4



5



6

division (p. 214 and Plate 6, fig. 33). A detailed study of one species, *Hypericum Androsaemum* L., revealed a more complete series of division figures which result in the formation of septa.

In the normal formation of the fiber-tracheid from the cambium the cell undergoes elongation, forms bordered pits, and develops a thick secondary wall. The nucleus of the protoplast, shown in figure 1, is elongate-oval in shape. In general the long axis conforms to the long axis of the fiber-tracheid. Normally there are one or more nucleoli present. Following the normal maturation of the fiber-tracheid in this species, the protoplast remains active. This activity is expressed by the presence of mitotic division figures. Karyokinesis once initiated is followed by cytokinesis. In fixed material, spindle fibers are apparent in metaphase and in early anaphase (figs. 2, 3 and 7) and persist through the telophase (figs. 4 and 8) until the daughter nuclei are distinct. The cell plate is well defined in the telophase just before the daughter nuclei emerge (figs. 4, 5, 8 and 9). It appears to be formed by the equatorial expansion of the phragmoplasts which extend the cell plate and quickly intersect the walls of the cell. This is in accord with the type of cytokinesis found in all somatic tissue, the expression of which is dependent upon the dimension of the cell, the plane of division, and the location and size of the nucleus (5). The two daughter nuclei pass into a "resting" state migrating to the central position of the newly-formed compartments at apparently equal rates (fig. 6). The division is transverse to the axis of the cell instead of longitudinal as in the original cambial initial.

The septum is formed in the region of the cell plate during cytokinesis. In mature stages it is always thin, in contrast to the heavy secondary wall as may be seen in figure 6. In staining reaction it resembles the primary

wall of the original fiber-tracheid, although the delicate nature of the septum made inadequate the use of chemical tests and polarized light to determine definitely whether the septum is formed only of intercellular cement substance or whether it consists of the intercellular substance and two adjacent primary walls.

The septate condition of these fiber-tracheids may be distinguished in radial, tangential and occasionally in transverse sections. As far as can be determined, the formation of septa is not confined to any particular region, but may occur in any part of the secondary wood formed during a single growing season. Septa and nuclei are apparent in most of the fiber-tracheids. However, the mitotic figures associated with the formation of septa are infrequent.

The original fiber-tracheid has now become, by the formation of a septum, a septate fiber-tracheid containing two nuclei within the confines of the original cell walls. It has been suggested (14) that the presence of septa in fiber-tracheids indicates a stage "intermediate to parenchyma rather than to tracheal elements," but according to Bailey (7) internal septation, while not a "characteristic of fibers," is also not evidence of transition to parenchyma. This is true because of the fundamental difference in the ontogeny of the cell and the constitution of the secondary walls. Our evidence supports this last assertion, because in their ontogeny and later development these cells are true fiber-tracheids with characteristic secondary walls. The internal septations are a later development, which in no way alters the fundamental nature of the original cell. It is apparent that the fundamental difference between the formation of certain parenchyma and tracheal elements is one of the timing of division, which may or may not be characteristic of development and maturation of the cells within a species.

If the divisions which form septa occur before the secondary wall is laid down, a strand tracheid or a wood parenchyma strand would result. If the divisions occur after the formation of the secondary wall, a septate fiber-tracheid would be the result.

In the formation of septate fiber-tracheids there is also an element of timing of the division which may be significant. It would be interesting to know how long a cell may remain a nucleated fiber-tracheid before becoming a septate fiber-tracheid, and whether each nucleated fiber-tracheid is a potential septate fiber-tracheid. This is significant in view of the fact that these elements have been used as diagnostic criteria in classification. However, one must emphasize the fact that it has not been determined whether in a definite section of wood all the cells have reached their end point of development or have been stopped in some intermediate stage. Observations on these points by numerous workers will aid in giving a true significance to the use of these variable elements in classification.

The occurrence of cytokinesis in the formation of septate fiber-tracheids distinguishes these elements from the truly multinucleate fibers which occur, at times, in the phloem. The formation of the cells under discussion also differs from the formation of cells by the cambial initials of the higher plants (1), (2), (3), (4), (5) in that, while the protoplasts involved are capable of divisions within the original cell, the resultant cells or compartments do not undergo the normal maturation pattern of cells derived from the cambium.

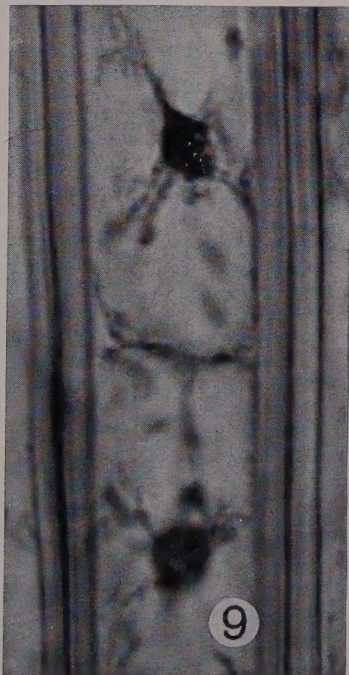
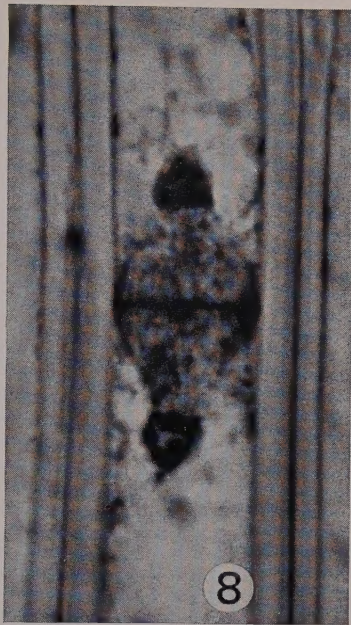
It is held by some (9, p. 153) that the protoplast disappears during the development of the lignified secondary wall of tracheary elements. Fuchs (11), in discussing the origin of lignin, suggests that the formation of lignin occurs only in those cells in which the protoplasm is

EXPLANATION OF THE ILLUSTRATION

FIGURE 7. Photomicrograph of metaphase division figure in fiber-tracheid. $\times$ ca. 1800.

FIGURE 8. Photomicrograph of telophase division figure in fiber-tracheid. $\times$ ca. 1800.

FIGURE 9. Photomicrograph of late telophase division figure in fiber-tracheid. $\times$ ca. 1800.





dying, while Griffioen (13) contends that although lignification is a vital process, it proceeds with the necrosis of the cell content and the death of the cell. In this connection, it is significant that, following the formation of a lignified secondary wall, the septate fiber-tracheids of *Hypericum Androsaemum* remain alive with a functionally active protoplast for a considerable period of time.

SUMMARY

The formation of septa in the fiber-tracheids of *Hypericum Androsaemum* L. is reported. The development of the fiber-tracheids is normal in that they undergo elongation and maturation of the secondary wall. However, the protoplast remains active and usually undergoes division at a right angle to the original division of the cambial initial. This division consists of true karyokinesis followed by cytokinesis. The septum is formed in the region of the cell plate and the daughter nuclei migrate to the central portion of the newly formed compartments. As far as can be determined, the formation of septa is not confined to any particular region, but may occur in any part of the secondary wood formed during a single growing season. The evidence is clear that the definition of a septate fiber-tracheid suggested by the Committee on Nomenclature of the International Association of Wood Anatomists is in agreement with the observable ontogeny and later development of the fiber-tracheid.

In conclusion, the authors wish to thank Professor R. H. Wetmore, under whose direction the original work was started, and Professor I. W. Bailey, for their helpful suggestions and active interest in this work.

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SOME NOMENCLATORIAL TRANSFERS AMONG PERUVIAN ORCHIDS

BY
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INCIDENT to working on the orchid flora of Peru, the following specific reductions were found advisable.

Elleanthus conifer *Reichenbach filius* in Walpers Ann. 6 (1862) 474.

Evelyna conifera Reichenbach filius & Warscewicz in Bonpl. 2 (1854) 113.

Elleanthus Weberbauerianus Kränzlin in Engler Bot. Jahrb. 54 (1916) Beibl. 117, p. 28.

Elleanthus conchophilus Schlechter in Fedde Repert. Beihefte 9 (1921) 46; in Beihefte 57 (1929) t. 103, Nr. 402.

A drawing from the type of *Evelyna conifera* from the Reichenbach Herbarium in Vienna has narrowly lanceolate leaves which are long-attenuate and up to about 22 cm. long and 2.5 cm. wide, a raceme about 6 cm. long and a lip which appears to be broadly rounded at the apex.

On the other hand, a photograph of the type of *Elleanthus Weberbauerianus* accompanied by floral analyses shows narrowly oblong-lanceolate acuminate leaves up to 14 cm. long and about 2 cm. wide, a raceme about 10 cm. long and a lip which is retuse at the apex.

However, a specimen (*Soukup 473*) apparently identical with *E. Weberbauerianus* has lanceolate-elongate-attenuate leaves up to 21 cm. long and 3.5 cm. wide, while the immature raceme is almost 7 cm. long. Another collection (*Macbride 3489*) has the leaf-blade of typical *E. Weberbauerianus*, up to only 15.8 cm. long, and a raceme about 8 cm. long. A further number (*Weberbauer 7868*) has leaves of both forms (elongate-lanceolate

and oblong- or elliptic-lanceolate) up to 19.5 cm. long and 4.3 cm. wide, and racemes up to about 9 cm. long.

Elleanthus conchochilus has somewhat smaller leaves (up to 11 cm. long and 2 cm. wide), a raceme up to 6 cm. long and floral segments (shown by analyses of the type as well as by the description) which are almost identical with those of *E. Weberbauerianus*.

Apparently the only noteworthy difference between the concepts is one of flower-color, *E. Weberbauerianus* being purple with white and brown lip and *E. conchochilus* said to be yellow.

It thus appears that these three concepts are specifically identical.

Elleanthus hymenophorus *Reichenbach filius* in Walpers Ann. 6 (1862) 480.

Evelyna hymenophora Reichenbach filius in Bot. Zeit. 10 (1852) 710.

Evelyna discolor Reichenbach filius & Warscewicz in Bonpl. 2 (1854) 113.

Elleanthus discolor Reichenbach filius in Walpers Ann. 6 (1862-3) 480-1.

In his original description of the Peruvian *Evelyna discolor*, Reichenbach cites as the more obvious differences from the related *E. hymenophora* the violet under side of the foliage, the erect inflorescence, the denticulate (not entire) keels on the lateral sepals, the broader more denticulate lip and the erect triangular acute (not retuse) rostellum.

A specimen of the type number of *Evelyna discolor* in our herbarium does not show any noticeable difference in coloration between the leaf surfaces, and the floral parts appear to match those of *E. hymenophora*, with the keels on the lateral sepals entire or nearly so. Moreover, an authentic specimen of the Central American *Ellean-*

thus *hymenophorus* from the Reichenbach Herbarium has a nearly erect raceme as in *E. discolor*, while a floral analysis on the same sheet shows a suborbicular dentate lip and the triangular tip to the rostellum described for *E. discolor*. Furthermore, a series of specimens of *E. hymenophorus* in our herbarium shows more or less erect racemes.

As now conceived, *Elleanthus hymenophorus* extends from Costa Rica, through Panama and Colombia to Peru.

***Altensteinia fimbriata* Humboldt, Bonpland & Kunth** Nov. Gen. et Sp. 1 (1816) 333, t. 72.

Altensteinia sceptrum Reichenbach filius Xen. Orch. 1 (1854) 18, *nomen subnudum*.

Altensteinia boliviensis Rolfe in Mem. Torr. Bot. Club 4 (1895) 265.

The concept *Altensteinia sceptrum* was in part separated from *A. fimbriata* by its twice larger stature; but, in view of the great variation in size in *A. fimbriata*, this distinction seems inconsequential. A further characterization attributed to *A. sceptrum* is that the lip is orbicular. However, a specimen in our herbarium bearing the data of the type collection of *A. sceptrum* shows the round-ovate lip common to *A. fimbriata*.

Altensteinia boliviensis was described as "a less vigorous plant" than *A. fimbriata*, "with distinctly smaller flowers." However, we have seen a Peruvian collection of *A. fimbriata* (*Macbride & Featherstone 1225*) which is an even smaller plant than typical *A. boliviensis* but has considerably larger flowers than that concept with a suborbicular, not elliptical, lip.

Another Peruvian collection (*Herrera 3503*) has measurements which appear nearly identical with those of *A. boliviensis*, but the lip is suborbicular, not elliptical as described.

Thus there does not appear to be any justification for the above segregations from the variable *A. fimbriata*, a species which appears to show many gradations in the form of the lip from suborbicular to round-ovate or round-elliptic.

***Altensteinia marginata* Reichenbach filius** Xen. Orch. 3 (1878) 20.

Prescottia pteristyloides Kränzlin in Engler Bot. Jahrb. 37 (1906) 393.

Altensteinia pterostyloides Schlechter in Fedde Repert. Beihefte 9 (1921) 126.

A careful comparison of these two concepts, as represented by records of the types as well as by the descriptions, indicate that they are conspecific.

The only discrepancies appear to be that *A. marginata* shows somewhat broader leaves than those of the type of *Prescottia pteristyloides*, and that the latter concept is noted as having narrowly lanceolate 1-nerved lateral sepals, whereas the lateral sepals of *A. marginata* are described as oblong and 3-nerved and are drawn as elliptic-lanceolate and 3-nerved. Both species came from regions of the same altitude.

***Altensteinia Matthewsii* Reichenbach filius** Xen. Orch. 3 (1878) 19.

Aa Matthewsii Schlechter in Fedde Repert. 11 (1912) 150.

Aa Lechleri Schlechter in Fedde Repert. Beihefte 9 (1921) 52; in Beihefte 57 (1929) t. 105, Nr. 411.

Judging from habit and analytical drawings of *Altensteinia Matthewsii* from the Reichenbach Herbarium in Vienna as well as from a specimen of that species identified by Reichenbach, it seems unwise to segregate from it the concept *Aa Lechleri*. Indeed the only discrepancy

between the concepts appears to be that *Aa Lechleri* is described as having longer lateral sepals than *Altensteinia Matthewsii*.

***Stenoptera acuta* Lindley** Gen. & Sp. Orch. Pl. (1840) 447—Cogniaux in Mart. Fl. Bras. 3, pt. 4 (1895) 252, t. 59, fig. 1.

Stenoptera elata Schlechter in Fedde Repert. Beihefte 9 (1921) 54; in Beihefte 57 (1929) t. 86, Nr. 335.

A comparison of *Stenoptera acuta*, as represented by a photograph of that species from the Lindley Herbarium at Kew, as well as by the detailed description and figure in Cogniaux's treatment of *S. acuta* (l.c.), shows that it cannot reasonably be separated from *S. elata* as represented by the description and figure (l.c.).

In fact the only discrepancies between the two concepts seem to be that *S. elata* is described as a rather taller plant with somewhat larger leaves and longer spike than *S. acuta*.

A Peruvian specimen referable to *S. acuta* (*Weberbauer 7583*) is almost as tall as *S. elata* and has even longer leaves than that concept.

PERU: Ayacucho, Prov. Huanta, Choimacota Valley, at 3000 meters altitude, "evergreen bush-wood", flowers greenish, February 28-March 10, 1926, *A. Weberbauer 7583*; Road from Tambo above Osno to the Apurimac, at 2800-3000 meters altitude, June 1910, *Weberbauer 5651*.—Huánuco, Cuzco (ex Kränzlin) fide Schlechter. Also Brazil (type) and Bolivia.

***Stenoptera pilifera* (HBK.) C. Schweinfurth**
comb. nov.

Altensteinia pilifera Humboldt, Bonpland & Kunth
Nov. Gen. et Sp. 1 (1816) 333, t. 73.

Stenoptera cardinalis Lindley Gen. & Sp. Orch. Pl. (1840) 448.

Porphyrostachys pilifera Reichenbach filius Xen.
Orch. 1 (1854) 18.

Spiranthes orchioides sensu Kränzlin in Engler Bot.
Jahrb. 26 (1899) 499, non A. Richard.

Since it appears wise to transfer this concept to the
genus *Stenoptera*, the specific epithet *pilifera* must be
used instead of the more lately applied adjective *cardin-*
alis.

The species appears to be widely distributed in Peru,
as well as occurring in Ecuador.

A NOTABLE EXTENSION OF RANGE OF
EPIDENDRUM ONCIDIOIDES
VAR. GRAVIDUM

BY
CHARLES SCHWEINFURTH

IT is interesting to report the occurrence in the West Indies of *Epidendrum oncidoides* Lindl. var. *gravidum* (Lindl.) A., H. & S.

The first West Indian collection of this widespread Central American form is here recorded from Cuba, Province of Oriente, Loma del Gato, September 1935, *Julian Acuña s.n.*

A second West Indian collection of this plant is from Puerto Rico. It is recorded from Maricao, growing on a stump, June 1939, *A. G. Kevorkian 6177*. The flowers are noted as being yellowish-green but do not expand at this station. In this latter particular they resemble those of the type of *E. gravidum* Lindl. which was collected in Mexico.

Epidendrum oncidoides was described from Brazil, but has been recorded from various parts of South and Central America and from Cuba.

A NOMENCLATORIAL TRANSFER

BY

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Maxillaria ampliflora *C. Schweinfurth nom. nov.*

Camaridium grandiflorum Ames in Proc. Biol. Soc. Wash. 34 (December 1921) 149, non *C. grandiflorum* Schltr. in Fedde Repert. Beihefte 9 (September 1921) 165.

As recent studies have convinced us that the concepts *Camaridium* and *Maxillaria* are congeneric, the Central American plant described as *Camaridium grandiflorum* Ames should, in our opinion, be referred to the genus *Maxillaria*. The prior use of the combination *Maxillaria grandiflora* by Lindley necessitates a new name.

This species was originally described from the Province of Chiriquí, Panama, (*E. P. Killip* 3565); but a fragmentary specimen from San Jerónimo, Costa Rica (*M. Valerio* 2709) is also referable to *Maxillaria ampliflora*.

Closely allied species are *Maxillaria semiorbicularis* A. & S. and ***M. planicola*** *C. Schweinfurth nom. nov.* (*Camaridium latifolium* Schlechter in Fedde Repert. Beihefte 17 (1922) 74, non *Maxillaria latifolia* Lindl.) which grows in low places. *M. semiorbicularis* differs in having a dissimilar lip with relatively large lateral lobes and *M. planicola* differs in having prominent pseudobulbs, distinctly petioled leaves and obtuse lateral lobes of the lip.